

INVENTORY OF THE VASCULAR FLORA OF THE BLAST ZONE, MOUNT ST. HELENS, WASHINGTON

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ABSTRACT

Mount St. Helens is an active volcano located in the Cascade Range of southwestern Washington. The volcano erupted in 1980 and created a wide array of devastated landscapes. Since the eruption, vegetation has been colonizing these new landscapes. In the summers of 1993 and 1994 we inventoried plant species and their relative abundance on the Pumice Plain, Plains of Abraham, Toutle Debris Avalanche, Toutle Ridge, and the crater. We distinguished plants as those found in primary successional uplands and wetlands and in refugia. Refugia are defined as habitat where plants survived the eruption as rootstock. The principal refugia are located between the Pumice Plain and Plains of Abraham.

The current flora is dominated by wind-dispersed invasive species, mainly those in the families Asteraceae, Poaceae, Cyperaceae, and Onagraceae. Large-seeded, late-successional understory species are common in refugia and, to a limited extent, have spread into primary substrates. The species documented comprise 341 species in 178 genera and 53 families. These species comprise 4 Sphenophyta, 6 Pterophyta, 9 Coniferophyta, and 322 Anthophyta (221 Dicotyledonae and 101 Monocotyledonae). Fifty-seven of the species are non-native. Species were surveyed for relative abundance on a three way scale—widespread, locally common, and infrequent. This checklist provides a baseline to judge future composition of the flora and plant invasion patterns.

Mount St. Helens is an active volcano located in the Cascade Range of southwestern Washington in the southern Cascade physiographic Province (46°12'N, 122°11'W). Pre-eruption forests were typical of the montane *Abies amabilis* (Douglas) James Forbes zone (Franklin and Dyrness 1988). After 130 years of inactivity, a major series of eruptions occurred beginning with a violent eruption on 18 May 1980. These eruptions created a diversity of devastated landscapes, and since the eruption, vegetation has been slowly colonizing these new landscapes. The many studies that have been conducted on Mount St. Helens have dramatically increased our understanding of primary successional processes, i.e., the patterns of revegetation of a devastated landscape (del Moral and Bliss 1993; del Moral et al. 1995; del Moral and Wood 1993a, b; Frenzen et al. 1994; Tsuyuzaki and Titus 1996; Wood and del Moral 1987, 1988). However, since no baseline inventory of the taxa present on the mountain has been available for use in assessments of the vegetation, we inventoried the vegetation of the primary-suc-

cessional substrates on the mountain to provide a base-line species list for future studies.

Cascade Range volcanoes are isolated from other areas of similar elevation. These volcanoes are high elevation islands surrounded by mountain ranges which are more than 1000 m below the volcanic peaks. Thus, a species list of Mount St. Helens vegetation may also be useful in understanding the biogeography of the Cascades volcanoes.

Plant inventories of primary successional environments on volcanoes are infrequent. Tsuyuzaki (1995) provides a species list for Mt. Usu in Japan, which erupted in 1977 and 1978. Other Cascade volcanoes, which erupted thousands of years ago, have been surveyed and the results are contained in Burnett (1985) for Mt. Hood, Wynd (1936) and Applegate (1939) for Mt. Mazama (Crater Lake), Cooke (1940) for Mt. Shasta, Gillett et al. (1961) and Oswald et al. (1995) for Mt. Lassen, Ireland (1968) for the Three Sisters, Jones (1938) for Mt. Rainier, and St. John and Hardin (1929) for Mt. Baker. Other primary successional environments are occasionally inventoried, such as the Thompson and Wade (1991) checklist of the vegetation of a 12-year-old surface-mined coal area in Kentucky.

Plants that successfully invade primary successional landscapes usually have seeds which are

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dispersed over long distances. These small, aerially-dispersed seeds, however, are only marginally capable of developing viable seedlings under harsh conditions. Large-seeded species, although more adapted to surviving as seedlings under harsh conditions, are slower to reach these devastated landscapes (Wood and del Moral 1987; del Moral 1993; del Moral and Bliss 1993). Plants which invade these landscapes fall into groups of functional traits (Tsuyuzaki and del Moral 1995). Functional traits are attributes or life history characteristics that groups of species exhibit in response to similar environmental pressures, and can be used to infer constraints imposed by the environment. Thus, an inventory of the species present on Mount St. Helens provides an opportunity to study ecological traits of invading species.

ENVIRONMENTAL CONDITIONS ON MOUNT ST. HELENS

Climate. The climate of the Mount St. Helens area is montane maritime, i.e., cool, wet winters with a significant snowpack at higher elevations, and warm dry summers. The climate is characterized by abundant yearly precipitation and short periods of drought, typically in July and August. Annual precipitation averages 2373 mm, yet often less than 5% of this falls between June and August. The snow-free growing season extends from April or May until late September, but it usually begins in June and ends by early September. Temperatures range from mean monthly minima of -4.2°C in January and 7.3°C in August to maxima of 0.5°C in January and 22.2°C in July (Spirit Lake Ranger Station (987 m), Anon. 1969; Reynolds and Bliss 1986). Summer temperatures range from 0 to 35°C with a mean ca. 12°C (Reynolds and Bliss 1986). Considerable variation is an important aspect of the Mount St. Helens climate. Precipitation shows dramatic annual variation for the summer months of July and August. Surface soil temperatures are often high on the devastated landscapes, approaching 50°C on tephra surfaces near Spirit Lake (Reynolds and Bliss 1986).

The eruption. The eruption of May 18, 1980, created a wide range of disturbances including tephra (all airborne materials ejected from a volcano, in this case pumice of different sizes), pyroclastic flows (masses of hot dry rock flowing suspended in air), hot airblasts, and lahars (unsorted mud and debris flows). Some of the features created by these disturbances include a pyroclastic flow into Spirit Lake, a 550 km² area of blown-down trees bordered by 96 km² of scorched trees, a 60 km² debris avalanche, and massive mudflows down the major streams draining the area (Lipmann and Mullineaux 1981). Most areas in the perimeter of the devastation were salvage logged and replanted. Because the major force of the eruption was directed laterally to the north, vegetation on the southern flank

of the volcano was not destroyed except in a few locations by lahars. The eruption reduced the height of the cone from 2950 m to 2550 m.

The focus of this study is on those areas where the vegetation was essentially eliminated and re-vegetation was dependent upon the dispersal of propagules from outside the site. These areas are: the Pumice Plain directly north of the cone; the Plains of Abraham to the east of the cone; refugia areas with surviving plants between the Pumice Plain and the Plains of Abraham; the crater breach area where the crater wall was demolished by the lateral eruption; the crater proper, which contains the lava dome; the Toutle Debris Avalanche; and Toutle Ridge between the North and South forks of the Toutle River (Fig. 1). The Pumice Plain, Toutle Debris Avalanche, and the breach contain a variety of both upland and wetland habitats. The Toutle Ridge contains refugia where the vegetation was shielded from the blast. The refugia between the Pumice Plain and Plains of Abraham contains many species which survived the eruption as rootstock.

Pumice Plain

The Pumice Plain ranges in elevation from 1150 to 1300 m and occupies an area of approximately 20 km² immediately north of the crater. This area was formed by the deposit of over 100 m of material from the debris avalanche, subsequent pyroclastic flows, and incandescent pumice depositions. It was also repeatedly impacted by later lahars (Lipmann and Mullineaux 1981). The current surface is generally flat or gently sloping with numerous gullies formed by water-erosion dissecting the surface. Before the eruption, the Pumice Plain was vegetated by open coniferous forest (Kruckeberg 1987) with timberline 600–800 m below its climatic limit (Lawrence 1938). Now the area is blanketed by pumice ranging in depth from 10 to 200 m (Lipmann and Mullineaux 1981). Surface pumice particles range in size from 1 mm to 10 cm. Surface colors range from light to dark gray with high surface albedo (Reynolds and Bliss 1986). The surface layer of pumice acts as a mulch that impedes evaporation from below; thus, considerable moisture may be present at lower depths while surface layers may be very dry. In the summer, the surface pumice dries quickly between rains. Therefore, most Pumice Plain habitats probably do not remain moist long enough to allow seedling establishment. At greater depths, however, the soil remains moist so that adult plants rarely suffer from drought (Reynolds and Bliss 1986; Chapin and Bliss 1988; Pfitsch and Bliss 1988; del Moral and Bliss 1993). Substrates with fine particles contain more moisture than areas with coarse particles, and the erosion rills were slightly moister than other microsities (del Moral and Bliss 1993). The Pumice Plain soils are pedologically immature with very low concentrations of N, K, P, organic matter, and microbial biomass (Nuhn 1987; Halvorson et al. 1991, 1992).

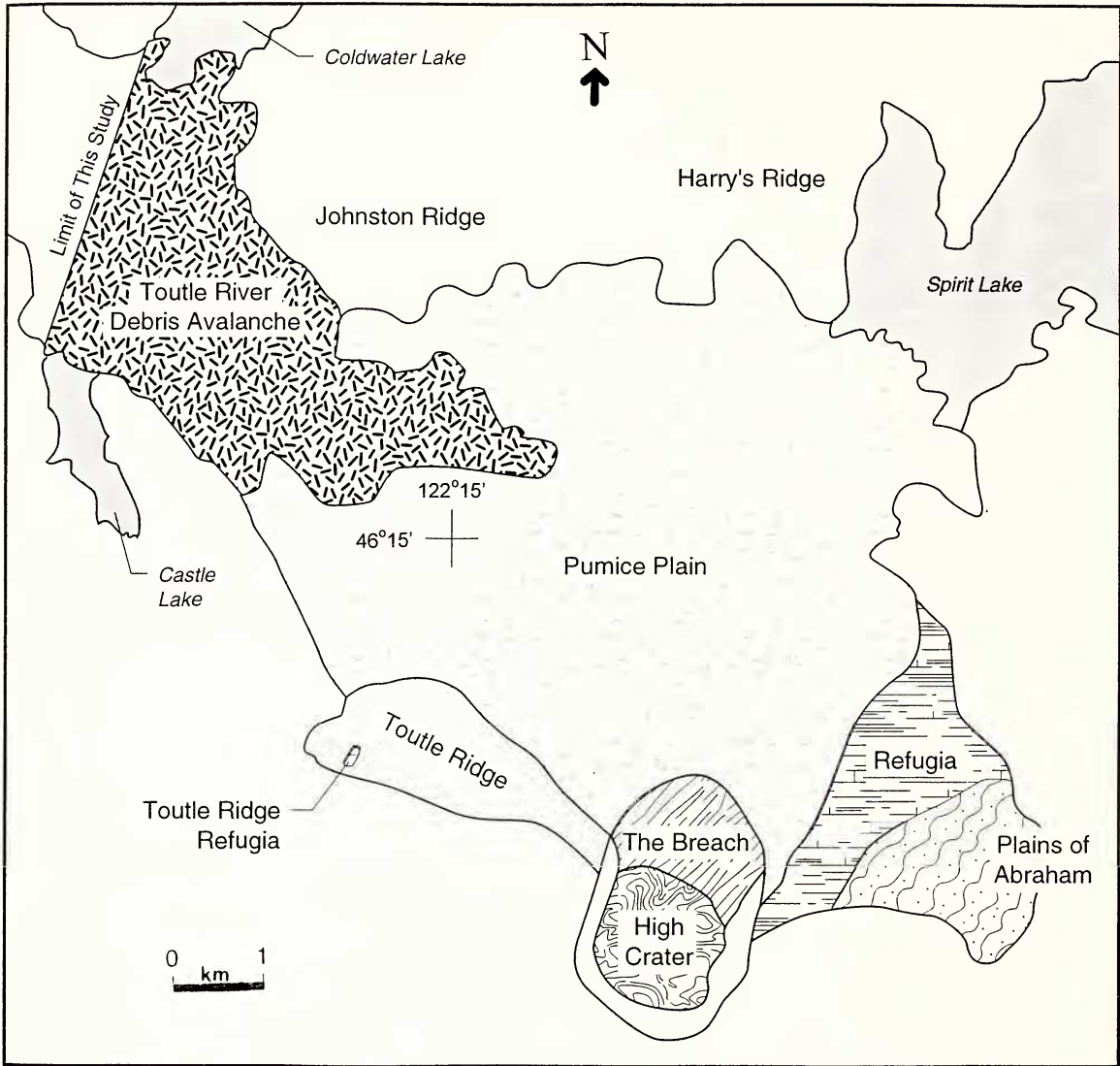


FIG. 1. Map of the study areas on Mount St. Helens, Washington.

Although seed sources for the Pumice Plain are distant (>3 km), the seed rain is dense with the seeds of species commonly found in upwind clearcuts (del Moral and Bliss 1993). In the post-eruption landscape, vegetation is sparse and was, until recently, confined to rills, but has now spread across the Plain. High surface soil temperatures and frequent summer droughts may explain why seedling establishment has been very low in many places on the Pumice Plain since the eruption (del Moral and Bliss 1993).

Four upland habitat types were recognized on the Pumice Plain by del Moral et al. (1995). These were refugia, pumice barrens, pyroclastic surfaces, and drainages. In this study refugia are treated as a separate habitat type, and the other three upland habitats were combined due to high floristic simi-

larity. Scattered on the pyroclastic and stable drainage surfaces are sites that developed dense patches of *Lupinus lepidus* Douglas within two years after the eruption. Initially, these patches were nearly monospecific, but eventually they created biological oases that facilitated invasions of open-site species (Wood and Morris 1990; del Moral 1993; del Moral and Wood 1993a). Since the large seeds of *L. lepidus* are too heavy to be wind dispersed, the patches apparently originated from a few individuals which survived the eruption (Bishop 1996).

The wetland areas of the Pumice Plain are found primarily along permanent and seasonal creeks and in or near springs. Both hot and cold water springs are found near Spirit Lake and both support lush wetland vegetation. The waters of Spirit Lake itself support aquatic vegetation.

Refugia

Refugia exist on north-facing slopes close to the cone. During the eruption, these snow-covered areas provided refuge for many species and enabled them to survive the eruption as rootstock, particularly late-successional forest understory species. These areas were usually steep, and thus erosion quickly removed the pumice layer and exposed the rootstock for resprouting. Refugia have also been invaded by open-site species characteristic of the Pumice Plain (del Moral et al. 1995). Soils of refugia are richer in nutrients than the Pumice Plain (J. H. Titus unpublished) and contain mycorrhizae, which are essential to the survival of many of the late-successional forest understory species (Titus 1995).

Plains of Abraham

The Plains of Abraham is at an elevation of 1400–1450 m in an area of gentle topography, and was barren prior to the eruption (Kruckeberg 1987). Although the main fury of the 1980 eruption was directed northward, the Plains of Abraham, located to the east of the cone, was also devastated by the blast and the resulting pyroclastic flows and lahars (Foxworthy and Hill 1982). In 1980 the Plain was covered by tephra and pockets of silt, and vascular plants were absent. By 1987 wind erosion had removed all fine materials so that the surface now consists of coarse pumice generally 2–5 cm in diameter. Water erosion initiated numerous shallow rills in the pumice-dominated landscape. The pumice on the Plains of Abraham is of pre-1980 origin. Thus soil nutrient levels are higher than on the Pumice Plain because the substrate was formed prior to the most recent eruption (del Moral and Bliss 1993). As on the Pumice Plain, rills were moister than surrounding flat sites, and fine textured soils had twice the moisture content of coarse soils (del Moral and Bliss 1993). Over time, the pumice weathers to a fine sand. Wind removes much of this material so that a “desert pavement” is formed. Areas not eroded by water are essentially smooth, lack sites where seeds might lodge, and dry rapidly. Primary succession on the Plains of Abraham is proceeding under highly stressful conditions, and plant cover is still relatively sparse. Microsite variation is distinct with plants much more prevalent on rill edges (del Moral and Wood 1993a).

Toutle River Debris Avalanche

The debris avalanche was formed by a massive landslide of the north flank of the mountain that occurred during the eruption. The debris material averages 45 m in depth, 2 km in breadth, and extends 25 km from the crater along the North Fork of the Toutle River (Lipman and Mullineaux 1981). Plant devastation on the debris avalanche was virtually complete (Adams et al. 1982); however, rare

individuals of at least 20 species survived on the debris deposit, the most widespread being *Epilobium angustifolium* L. ssp. *circumvagum* Mosq., *Cirsium arvense* (L.) Scop., and *Lupinus latifolius* J. Agardh. These individuals apparently resprouted from plant fragments that had been transported by the debris slide. The most common woody species to survive were willows, which regenerate readily from root and stem fragments. These willows were found primarily in the western portion of the avalanche and farthest from the crater (Dale 1986). Recovery of the vegetation was initiated within the first year after the eruption, and rapid colonization by *Alnus rubra* Bong. and other riparian species has occurred since that time (Adams et al. 1987). Recovery has been slow in other areas, however, especially in areas closer to the mountain. The primary seed source for the debris avalanche is seed rain from adjacent scorched pre-eruption clearcuts, heavily vegetated by herbaceous perennials that produce copious light, wind-dispersed plumed seeds (Franklin et al. 1985; Dale 1989).

Debris avalanche soils have an adequate balance between moisture retention and aeration properties, and percent organic matter is low but adequate for plant growth (Adams and Dale 1987). The soils are sandy or silty sand with the greater than 2 mm fractions comprising about 65% of soil samples.

A massive reseeding effort was conducted in 1980 and 1981 on the Toutle River debris avalanche using non-native grasses and forbs to reduce erosion. Many of the seeded species did not grow well on the new substrates, and there is no evidence that erosion was reduced (Dale 1989; Tsuyuzaki 1995). However, many other seeded species survived and now dominate much of the mudflow. This dominance by invasive non-native species may be slowing natural succession. Our survey was conducted on the eastern portion of the mudflow and terminated at a line roughly connecting the south side of Coldwater Lake to the northwest side of Castle Lake. This boundary line is at an elevation of approximately 760 m (Fig. 1) and was selected so as to avoid heavily artificially seeded areas. Much of the habitat west of our study area is dominated by non-native species, particularly legumes.

Wetlands on the Toutle debris avalanche appear to be unique and have not been studied. Four distinct types can be distinguished based on hydrological and physical characteristics. Deep potholes created by large masses of entrained ice are now occupied by wetlands composed of temporary snow melt and rain water ponds or permanent spring-fed ponds. Broad cattail-dominated marshes spread across the mudflow. Riparian vegetation along many creeks is abundant, and numerous springs on the mudflow support a diverse flora. Two types of riparian habitat are found on the debris avalanche: unstable riparian areas that support a sparse herbaceous veg-

etation, and more stable riparian areas dominated by dense willow thickets.

Toutle Ridge

Toutle Ridge is an elevated area located between the North and South Forks of the Toutle River. This area was devastated by the eruption, although in a somewhat peripheral manner similar to that of the Plains of Abraham. There are two small refugia on the Ridge, but no wetlands. The study area ends to the west of the Ridge where blown-down trees are common and the devastation was less intense.

Crater

Since the creation of a crater by the eruption of 1980, a lava dome has been growing in its center. The crater can be separated into two parts: the breach, which is a wide area where the lateral eruption removed the north face of the mountain, and the high crater, which contains the lava dome. The breach contains both upland and wetland habitats from small springs. Creek banks are too unstable to support vegetation. The high crater is mostly barren upland. Very small wetland areas were created on the lava dome where stream from fumaroles continues to condense. These condensation areas principally support moss and algae, but a few wind dispersed vascular plants have also colonized these unusual sites.

METHODS

Census technique. To complete the current inventory, surveys were conducted during the summers of 1993 and 1994. The entire inventory area was examined several times over the season, and locations were recorded for all species present. The species list was compiled from observations noted during these surveys. Species were categorized into three abundance categories: widespread, locally common, and infrequent. These are qualitative rankings and are not based on quantitative data although in some cases quantitative data assisted in assigning the abundance rank. "Widespread" indicates that the plant was abundant throughout the inventory area. "Locally common" indicates a plant that was only locally common or occasionally a plant with a more scattered distribution. "Infrequent" describes plants which were difficult to detect.

Determinations and nomenclature. Species determinations were made using the *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973) with updated nomenclature from *The Jepson Manual: Higher Plants of California* (Hickman 1993). Voucher specimens were deposited at the University of Washington herbarium.

Pre-eruption Conditions

Before 1980, the 2950 m Mount St. Helens was surrounded by a patchwork of forested and clearcut

land in varying stages of reforestation. The forests were typical of the *Abies amabilis* zone (Franklin and Dyrness 1988), composed primarily of *Abies amabilis*, *Abies procera* Rehder, *Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*, and *Tsuga heterophylla* (Raf.) Sarg. (Lawrence 1938). Clearcut land was generally replanted with *P. menziesii* and *A. procera* seedlings and had a lush cover dominated by herbs (e.g., *Epilobium angustifolium* and *Anaphalis margaritacea* (L.) Benth. & Hook.) and shrubs (e.g., *Acer circinatum* Pursh and *Rubus ursinus* Cham. & Schldl.). The riparian vegetation along the Toutle River was comprised primarily of deciduous trees (*Alnus rubra*, *Populus balsamifera* L. ssp. *trichocarpa* (Torrey & A. Gray) Brayshaw, *Salix scouleriana* Hook. and *Salix sitchensis* Bong.).

Before the eruption the vegetation on the Plains of Abraham was sparse (Kruckeberg 1987), and timberline was 600–800 m below its climatic limit. The forest that occurred was composed only of scattered conifers dominated by *Abies lasiocarpa* (Hook.) Nutt. var. *lasiocarpa*, *Polygonum newberryi* Small, and *Penstemon cardwellii* (Lawrence 1938).

Previous botanical exploration. The pre-eruption Mount St. Helens flora was considered to be depauperate in species richness in comparison with other Northwestern Pacific volcanic summits due to geologically recent eruptions and mudflows (Kruckeberg 1987; del Moral and Wood 1986, 1988). This geological activity caused the volcano to have a suppressed timberline (Lawrence 1954). Since the eruption, researchers have sought an accurate picture of the pre-eruption assemblage of individual plant species, the plant communities in which they resided, and how those plant communities related to other nearby volcanic massif communities. Unfortunately, no comprehensive flora exists. A relatively complete pre-eruption flora is inferred by inventories contained within three publications, *Flora of the State of Washington* (Piper 1906), *The Flora of Mt. St. Helens* (St. John 1976), and *Plant Life on Mount St. Helens before 1980* (Kruckeberg 1987).

The first organized botanical exploration of Mount St. Helens and vicinity was conducted in 1898 by Dr. F. V. Colville, principal botanist of the U.S. Department of Agriculture. However, no flora was published until Harold St. John researched Colville's journals and published a brief accounting (St. John 1976). According to the journal, Colville traveled and collected throughout Oregon and Washington. His collections of the Mount St. Helens area appear to be limited to the south side of the mountain since he approached from the south via the Lewis River, camped at Merrill Lake, and then proceeded up the Kalama River to Three Buttes Camp (1220 m) at the southwest base of Mount St. Helens on 19 August 1898. From there

he ascended and collected on the mountain. He listed 77 species; a partial collection of these are deposited at the Smithsonian Institution. Colville's flora remains unpublished, but his collection was used by C. V. Piper to construct a flora of the state of Washington, published by the U.S. National Herbarium in 1906 (Piper 1906).

The most comprehensive inventory of the Mount St. Helens flora was conducted in 1925 by Harold St. John and students including C. S. English, Jr. During an eleven-day visit in August 1925, they collected 315 plant species. Eight days were spent botanizing the region surrounding Spirit Lake and the north slope of the mountain, and one day climbing to the summit. An additional two days were spent collecting on the south side, exploring the upper valley of the Lewis River and the area around the present town of Cougar. The result of the inventory was not published until 1976, fifty years after the fieldwork was completed (St. John 1976). The collection is stored at the Washington State University Marion Ownbey Herbarium in Pullman, Washington.

The last documented botanical exploration of Mount St. Helens prior to the eruption was conducted in 1979 by Dr. Arthur Kruckeberg and eighteen members of the Washington Native Plant Society (Kruckeberg 1979). They identified approximately 86 plant species. They limited their investigation to timberline and above, beginning at Timberline Camp and the adjacent parking lot (1340 m—this area is now part of the Pumice Plain), and ascending to just below Sugar Bowl on the NE face (2075 m). Additional observations were made on a second day's traverse of Windy Pass (1495 m) and across the Plains of Abraham to the head of Ape Canyon (1280 m) on the southeast flank of the mountain.

DESCRIPTION OF CURRENT VEGETATION

Mount St. Helens is surrounded by thousands of hectares of recent clearcuts that are thickly vegetated with weedy wind-dispersed invasive species. The clearcuts provide a seed source for the recently created landscapes found on the volcano (del Moral and Bliss 1993). Thus, weedy invasive species typical of clearcuts were found at all sites examined during our surveys. Upland primary successional landscapes were similar in vegetation, except for the Toutle River Debris Avalanche which had additional dense stands of non-native legumes. The refugia have a vegetation distinct from the primary successional landscapes. Tree species were infrequent or only locally common. However, dense groves of trees did not occur on the Toutle River Debris Avalanche.

An unusual species that occurred in several of the areas was *Salix exigua* Nutt. This species generally occurs to the east of the Cascades. The probable cause for the presence of this species is that the open

TABLE 1. NUMBER OF NATIVE AND NON-NATIVE SPECIES IN HABITATS OF THE MOUNT ST. HELENS BLAST ZONE.

Habitat	Number of native species	Number of non-native species
Pumice Plain uplands	151	20
Pumice Plain wetlands	110	11
Refugia	160	10
Plains of Abraham	65	4
Toutle Debris Avalanche uplands	146	44
Toutle Debris Avalanche wetlands	114	42
Toutle Ridge uplands	86	5
Toutle Ridge refugia	93	6
Breach uplands	47	5
Breach wetlands	27	5
High Crater	14	3

primary successional habitats of Mount St. Helens provide colonization sites for widely dispersed wind-dispersed species such as *Salix* species.

Pumice Plain

Upland. The barren areas of the Pumice Plain are floristically consistent across the Plain and have low cover. *Anaphalis margaritacea*, *Hypochaeris radicata* L., *Lupinus lepidus*, *Epilobium angustifolium*, *Penstemon cardwellii* Howell, *Penstemon serifulatus* Menzies, *Hieracium albiflorum* Hook., *Carex mertensii* Prescott, *Carex spectabilis* Dewey, *Agrostis pallens* Trin., *Agrostis scabra* Willd., and *Juncus parryi* Engelm. are typically among the leading dominants in all barren sites. Densely vegetated areas of the Pumice Plain tend to be dominated by these same species. Across the barren areas of the Pumice Plain, *L. lepidus* also forms extensive densely vegetated patches. One hundred and seventy-three species were found on Pumice Plain uplands (Tables 1 and 2).

Wetland. *Juncus* and *Salix* species often dominate springs and wet areas, especially *Salix sitchensis* Bong., *Juncus bufonius* L., and *Juncus acuminatus* Michaux. *Equisetum arvense* L. also occupies broad wet areas. *Epilobium watsonii* Barbey, *Salix sitchensis*, and *Mimulus guttatus* DC. are common along creeks. The waters of Spirit Lake contain *Potamogeton natans* L., *Myriophyllum sibiricum* V. Komarov, and *Ranunculus aquatilis* L. Extensive algal mats occur in both thermal and cold water springs. Wetland areas are usually more thickly vegetated and diverse than upland areas. One hundred and twenty-one species were found in Pumice Plain wetlands.

Refugia

Refugia are dominated by woody species such as *Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) A. Löve & D. Löve, *Ribes laxiflorum* Pursh, *Rubus*

TABLE 2. CHECKLIST OF VASCULAR PLANT SPECIES IN PRIMARY SUCCESSIONAL HABITATS ON MOUNT ST. HELENS. w = widespread; c = locally common; i = infrequent; 1 = Pumice Plains uplands; 2 = Pumice Plain wetlands; 3 = Refugia; 4 = Plains of Abraham; 5 = Toutle Debris Avalanche uplands; 6 = Toutle Debris Avalanche wetlands; 7 = Toutle Ridge uplands; 8 = Toutle Ridge refugia; 9 = Breach uplands; 10 = Breach wetlands; 11 = High Crater; E = exotic non-native species.

Species	1	2	3	4	5	6	7	8	9	10	11
Cupressaceae											
<i>Thuja plicata</i>	i				i						
Pinaceae											
<i>Abies amabilis</i>	i		i		i		i	i	i		i
<i>Abies lasiocarpa</i>			i	i					i		i
<i>Abies procera</i>	i		i	i	c		c	w	i		i
<i>Pinus contorta</i> var. <i>latifolia</i>	i			i	i		i	i			
<i>Pinus monticola</i>	i				i						
<i>Pseudotsuga menziesii</i>	c		i	i	i		i	i			
<i>Tsuga heterophylla</i>	i		i	i	c		i	i			
<i>Tsuga mertensiana</i>			i	i							
Equisetaceae											
<i>Equisetum arvense</i>	c	w			c	w					
<i>Equisetum fluviatile</i>						i					
<i>Equisetum hyemale</i> ssp. <i>affine</i>		i				i					
<i>Equisetum palustre</i>						i					
Blechnaceae											
<i>Blechnum spicant</i>	i	i	i	i	i						
Dennstaedtiaceae											
<i>Pteridium aquilinum</i> var. <i>pubescens</i>			i		i						
Dryopteridaceae											
<i>Athyrium filix-femina</i>	c	i	c	i	c		i	c	c	c	
<i>Cystopteris fragilis</i>			i		i						
<i>Polystichum munitum</i>	c	i	c	i	c	i	i	c	c	c	
Pteridaceae											
<i>Cryptogramma cascadenis</i>	i		i	i					i		
Aceraceae											
<i>Acer circinatum</i>					i			c			
<i>Acer glabrum</i> var. <i>douglasii</i>			i					c			
<i>Acer macrophyllum</i>	i										
Apiaceae											
<i>Heracleum lanatum</i>			c								
<i>Lomatium martindalei</i>	i		c				w	i	i		
<i>Oenanthe sarmentosa</i>		i	i								
<i>Osmorhiza purpurea</i>			i					c			
Araliacene											
<i>Oplopanax horridum</i>			i								
Asteraceae											
<i>Achillea millefolium</i>	c		w	i	c		w	w	i		
<i>Agoseris aurantiaca</i>	i		i	i	i		c	i	i	i	
<i>Agoseris glauca</i> var. <i>glauca</i>	i		i	i	i		c	i	i	i	
<i>Agoseris grandiflora</i>	i		i		i		i	i			
<i>Agoseris heterophylla</i>	i	i									
<i>Anaphalis margaritacea</i>	w	c	w	w	w	i	w	w	w	w	c
<i>Antennaria rosea</i>	i		i		i		i				
<i>Antennaria umbrinella</i>	i				i		c				
<i>Arnica cordifolia</i> var. <i>cordifolia</i>	i		i				i	i			
<i>Arnica latifolia</i> var. <i>gracilis</i>	c		c	c			c	c	w		
<i>Arnica mollis</i>	i										
<i>Arnica nevadensis</i>	i								i		
<i>Aster brachyactis</i>		i				i					
<i>Aster frondosus</i>		i									
<i>Aster ledophyllus</i> var. <i>ledophyllus</i>	c	i	i	i	i		w	w	c		
<i>Aster modestus</i>			i								
<i>Cirsium arvense</i> var. <i>horridum</i> (E)	c	w	c		c	c	i	i	c	i	
<i>Cirsium vulgare</i> (E)	i	i	i		c	c					

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
<i>Conyza canadensis</i>	i	i			c	c					
<i>Crepis capillaris</i> (E)					i	i					
<i>Erigeron aliceae</i>	i	i	i		i	i					
<i>Erigeron peregrinus</i> var. <i>callianthemus</i>	i	i	i		i	i					
<i>Eriophyllum lanatum</i> var. <i>lanatum</i>	i		c		i				i		
<i>Gnaphalium canescens</i> ssp. <i>thermale</i>	c				c	i					
<i>Gnaphalium purpureum</i>					i	i					
<i>Gnaphalium uliginosum</i> (E)	i	c			w	w					
<i>Hieracium albiflorum</i>	w		w	w	w	i	w	w	w	i	i
<i>Hieracium gracile</i>	c			i					i	i	
<i>Hypochaeris radicata</i> (E)	w	w	w	w	w	w	c	w	w	i	i
<i>Lactuca muralis</i> (E)	i	i			i	i					
<i>Lactuca serriola</i> (E)					i	i					
<i>Lapsana communis</i> (E)					i	i					
<i>Leontodon taraxacoides</i> spp. <i>taraxacoides</i> (E)			i		i	i					
<i>Leucanthemum vulgare</i> (E)					c	i					
<i>Luina hypoleuca</i>	i		i	i							
<i>Petasites frigidus</i> var. <i>palmatus</i>	i	w	i		c	c			c	i	
<i>Senecio fremontii</i> var. <i>fremontii</i>	i										
<i>Senecio jacobaea</i> (E)	i				c	i		i	i	i	
<i>Senecio sylvaticus</i> (E)	w	i	i	i	c	c	i	i	c	i	i
<i>Senecio triangularis</i> var. <i>triangularis</i>	i				i						
<i>Senecio vulgaris</i> (E)	i										
<i>Solidago canadensis</i> ssp. <i>elongata</i>					i	i					
<i>Sonchus arvensis</i> (E)						i					
<i>Sonchus asper</i> ssp. <i>asper</i> (E)	i	w	i		i	w					
<i>Sonchus oleraceus</i> (E)						i					
<i>Taraxacum officinale</i> (E)	i		i		i	i					
<i>Trimorpha lonchophylla</i>		i									
Berberidaceae											
<i>Achlys triphylla</i> ssp. <i>triphylla</i>			i		i						
<i>Vancouveria hexandra</i>			c		i			c			
Betulaceae											
<i>Alnus rubra</i>	i		i		w	w					
<i>Alnus viridis</i> ssp. <i>sinuata</i>	w	i	w		i	i	i	w			
Boraginaceae											
<i>Myosotis laxa</i>					c	i					
Brassicaceae											
<i>Cardamine oligosperma</i> var. <i>oligosperma</i>			i		i	i					
<i>Cardamine pensylvanica</i>	i		c		i	i					
<i>Draba verna</i>					i	i					
<i>Rorippa curvisiliqua</i> var. <i>lyrata</i>		c			i	c					
<i>Rorippa nasturtium-aquaticum</i>		i				i					
<i>Rorippa palustris</i> var. <i>occidentalis</i>		i									
Callitrichaceae											
<i>Callitriche stagnalis</i> (E)						w					
Campanulaceae											
<i>Campanula rotundifolia</i>			i								
<i>Campanula scouleri</i>	i		c						i		
Caprifoliaceae											
<i>Linnaea borealis</i> var. <i>longiflora</i>									c		
<i>Lonicera ciliosa</i>					i						
<i>Sambucus racemosa</i> var. <i>arborescens</i>			w		i	i	i	w			
Caryophyllaceae											
<i>Arenaria serpyllifolia</i> ssp. <i>serpyllifolia</i> (E)	i		i	i	i	i					
<i>Cerastium arvense</i>			i		i				i		
<i>Cerastium nutans</i>			i		c	i			i		
<i>Moehringia macrophylla</i>		i			i	i			c		
<i>Sagina saginoides</i>		i				c					

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
<i>Silene parryi</i>	i										
<i>Spergula arvensis</i> ssp. <i>arvensis</i> (E)					i	i					
<i>Spergularia marina</i>						i					
<i>Spergularia rubra</i> (E)	i	i	i	i	i	i	i	i	i	i	i
<i>Stellaria borealis</i> ssp. <i>stichana</i>					c	c					
<i>Stellaria calycantha</i>	i	i	i		i	i					
<i>Stellaria crispa</i>	i	i	c		i	c	i	i			
<i>Stellaria nitens</i>					c	c					
Celastraceae											
<i>Paxistima myrsinites</i>					i						
Cornaceae											
<i>Cornus canadensis</i>					i			c			
Crassulaceae											
<i>Sedum oreganum</i>	i	i	i								
Ericaceae											
<i>Arctostaphylos nevadensis</i>	i		i	i			c	w			
<i>Arctostaphylos uva-ursi</i>								i			
<i>Gaultheria ovatifolia</i>			i		i						
<i>Gaultheria shallon</i>			c		i						
<i>Menziesia ferruginea</i> var. <i>ferruginea</i>			w								
<i>Orthilia secunda</i>					i						
<i>Phyllodoce empetriformis</i>			i								
<i>Pyrola asarifolia</i>			i								
<i>Rhododendron albiflorum</i>			i								
<i>Vaccinium membranaceum</i>	i		w	i	i		w	w			
<i>Vaccinium ovalifolium</i>			c				i	i			
<i>Vaccinium parvifolium</i>	i		i		i		i	i			
Fabaceae											
<i>Cytisus scoparius</i> (E)	i										
<i>Lotus corniculatus</i> (E)					w	c					
<i>Lotus purshianus</i> var. <i>purshianus</i>					w	w					
<i>Lupinus latifolius</i> var. <i>latifolius</i>	w	i	w	w	w	w	w	w			
<i>Lupinus lepidus</i> var. <i>lepidus</i>	w	i	i	w	w	w	w			i	
<i>Medicago lupulina</i> (E)					w	w					
<i>Melilotus alba</i> (E)					w	w					
<i>Trifolium microcephalum</i>					i						
<i>Trifolium pratense</i> (E)					w	w					
<i>Trifolium repens</i> (E)	i	i			w	w					
Gentianaceae											
<i>Centaurium erythraea</i> (E)					i	w					
Grossulariaceae											
<i>Ribes bracteosum</i>			i								
<i>Ribes howellii</i>			c						i		
<i>Ribes lacustre</i>	i		w				i	w			
<i>Ribes laxiflorum</i>			w				i	w			
<i>Ribes sanguineum</i> var. <i>sanguineum</i>					i						
<i>Ribes viscosissimum</i> var. <i>viscosissimum</i>			i								
Halagaraceae											
<i>Myriophyllum hippuroides</i>		i				i					
<i>Myriophyllum sibiricum</i>		i				i					
Hydrophyllaceae											
<i>Hydrophyllum fendleri</i> var. <i>albifrons</i>					i						
<i>Phacelia leptosepala</i>	c		c	i	i		c	c			
<i>Phacelia mutabilis</i>	i		i	i	i		i	i			
<i>Phacelia nemoralis</i> ssp. <i>oregonensis</i>	c		c	i	i		i	i			
Hypericaceae											
<i>Hypericum perforatum</i> (E)					i						

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
Onagraceae											
<i>Circaea alpina</i> ssp. <i>pacifica</i>						i					
<i>Epilobium anagallidifolium</i>	c		i	c	c	i	i	i	i	c	
<i>Epilobium angustifolium</i>	w	w	w	w	w	w	i	i	w	w	i
<i>Epilobium brachycarpum</i>	c	i			w	w			c		
<i>Epilobium ciliatum</i> ssp. <i>ciliatum</i>	i	w	i		c	w				w	
<i>Epilobium clavatum</i>	c	i	i	i			i	i	i	c	
<i>Epilobium glaberrimum</i> ssp. <i>fastigiatum</i>	i	i	i		i	i			i	i	
<i>Epilobium glaberrimum</i> ssp. <i>glaberrimum</i>	i	i	i		i	i					
<i>Epilobium hornemannii</i> ssp. <i>hornemannii</i>	i	i	i						i	i	
<i>Epilobium lactiflorum</i>	i	i	i						i	i	
<i>Epilobium luteum</i>		i	i								
<i>Epilobium minutum</i>	c	i			c	i					
Oxalidaceae											
<i>Oxalis oregana</i>					i						
Papaveraceae											
<i>Dicentra formosa</i>	i		i								
Plantaginaceae											
<i>Plantago lanceolata</i> (E)	i					i					
<i>Plantago major</i> var. <i>major</i> (E)						i					
Polemoniaceae											
<i>Collomia heterophylla</i>					w	c					
<i>Collomia larsenii</i>							c				
<i>Collomia tinctoria</i>					i	i					
<i>Phlox diffusa</i>			i				w				
<i>Phlox gracilis</i>					i	i					
Polygonaceae											
<i>Eriogonum pyrolifolium</i> var. <i>coryphaeum</i>	w		i	w			w		i		
<i>Polygonum douglasii</i> ssp. <i>douglasii</i>	i				i						
<i>Polygonum minimum</i>	w	i	c	i	c	c	w	i			
<i>Polygonum newberryi</i>				i			w	i			
<i>Polygonum persicaria</i> (E)						i					
<i>Rumex acetosella</i> (E)	i		i			i	w	w			
<i>Rumex crispus</i> (E)						i					
<i>Rumex obtusifolius</i> (E)						i					
Portulacaceae											
<i>Calyptidium umbellatum</i> var. <i>caudiciferum</i>	w			w			w	i	w		i
<i>Claytonia lanceolata</i> var. <i>lanceolata</i>			i								
<i>Claytonia sibirica</i>		i	c		i	i		c			
<i>Montia parvifolia</i> var. <i>parvifolia</i>	w	c	i		i	i					
Primulaceae											
<i>Trientalis latifolia</i>			i		i						
Ranunculaceae											
<i>Actaea rubra</i>			i					i			
<i>Aquilegia formosa</i>			w								
<i>Ranunculus aquatilis</i> var. <i>capillaceus</i>		c				c					
<i>Ranunculus aquatilis</i> var. <i>hispidulus</i>		c				c					
<i>Ranunculus sceleratus</i> var. <i>sceleratus</i>		c				i					
<i>Trautvetteria caroliniensis</i> var. <i>occidentalis</i>			i								
Rosaceae											
<i>Amelanchier alnifolia</i>			c				i	i			
<i>Aruncus dioicus</i> var. <i>pubescens</i>	i		w	i	i		i	c			
<i>Fragaria virginiana</i> ssp. <i>platypetala</i>	i		w	i	c	c	w	w	i		
<i>Holodiscus discolor</i>	i				i						
<i>Luetkea pectinata</i>	w		w	w			w	i	c	w	
<i>Potentilla anserina</i> ssp. <i>anserina</i>						w					

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
<i>Potentilla glandulosa</i> ssp. <i>glandulosa</i>	i										
<i>Prunus emarginata</i>					i						
<i>Rosa gymnocarpa</i>	i		i		i			i			
<i>Rubus discolor</i> (E)					i						
<i>Rubus idaeus</i> var. <i>gracilipes</i>					i						
<i>Rubus laciniatus</i> (E)					i						
<i>Rubus lasiococcus</i>	i		w	i	i		c	w			
<i>Rubus leucodermis</i>			i		i			i			
<i>Rubus parviflorus</i>	i		w	i	i		i	c			
<i>Rubus spectabilis</i>	i		w	i	i		i	w			
<i>Sibbaldia procumbens</i>							c				
<i>Sorbus sitchensis</i> var. <i>grayi</i>			w				i	w	i		
<i>Spiraea betulifolia</i>			i		i						
<i>Spiraea densiflora</i> var. <i>densiflora</i>			i								
<i>Spiraea douglasii</i>			i								
Rubiaceae											
<i>Galium asperrimum</i>					i						
<i>Galium triflorum</i>					i						
Salicaceae											
<i>Populus balsamifera</i> ssp. <i>trichocarpa</i>	c	i	i	i	w	c	i	i			
<i>Populus tremuloides</i>					c						
<i>Salix commutata</i>	i	i									
<i>Salix exigua</i> ssp. <i>exigua</i>		i			i	i					
<i>Salix geyeriana</i>					i	i					
<i>Salix lucida</i> ssp. <i>lasiandra</i>	i	c	i		i	c					
<i>Salix scouleriana</i>	i	i	i		i	i					
<i>Salix sitchensis</i>	w	w	w	c	w	w	w	c	c	c	i
Saxifragaceae											
<i>Heuchera glabra</i>	i	i	i		i	i					
<i>Heuchera micrantha</i>	i	i	i								
<i>Mitella breweri</i>	i	i	c								
<i>Mitella pentandra</i>	i	i	c								
<i>Saxifraga arguta</i>		i	i								
<i>Saxifraga ferruginea</i> var. <i>macounii</i>	w	i	w	w	c		i		c		
<i>Saxifraga tolmiei</i> var. <i>tolmiei</i>	i		i								
<i>Tellima grandiflora</i>			c								
<i>Tiarella trifoliata</i> var. <i>unifoliata</i>	i		c					c			
<i>Tolmiea menziesii</i>	i	i	c		i	i					
Scrophulariaceae											
<i>Castilleja miniata</i> ssp. <i>miniata</i>	c		w		i	i	w	w			
<i>Digitalis purpurea</i> (E)					i						
<i>Mimulus floribundus</i>		i									
<i>Mimulus guttatus</i>		c				c					
<i>Mimulus lewisii</i>		c	w								
<i>Nothochelone nemorosa</i>	c		c	i	c	i	c	c			
<i>Parentucellia viscosa</i>					i	c					
<i>Pedicularis racemosa</i> var. <i>racemosa</i>	i		i				c				
<i>Penstemon cardwellii</i>	w		w	w	w		w	w	i		
<i>Penstemon confertus</i>							i				
<i>Penstemon rupicola</i>	i		i								
<i>Penstemon serrulatus</i>	w		c	i	c	i	c	c			
<i>Verbascum thapsus</i> (E)					i						
<i>Veronica americana</i>						c					
<i>Veronica officinalis</i> (E)					i	c					
<i>Veronica serpyllifolia</i> ssp. <i>humifusa</i>					i	i					
Valerianaceae											
<i>Valeriana sitchensis</i> ssp. <i>sitchensis</i>			w					w			
Violaceae											
<i>Viola sempervirens</i>	i		c		i	i	i	i			

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
Cyperaceae											
<i>Carex canescens</i>		i			i	i					
<i>Carex deweyana</i> ssp. <i>leptopoda</i>					i						
<i>Carex illota</i>	i										
<i>Carex lenticularis</i> var. <i>lipocarpa</i>		i				c					
<i>Carex leporinella</i>	i										
<i>Carex mertensii</i>	w	w	w	w	w	w	w	w	w	w	i
<i>Carex microptera</i>	w	w	c	w	w	i	w	c	c		
<i>Carex ovalis</i>	i										
<i>Carex pachystachya</i>	w	c	i	w	i	c	c				
<i>Carex paysonis</i>	w	c	w	w			w	w	i	i	i
<i>Carex phaeocephala</i>	c	c		i							
<i>Carex praticola</i>	c	i	c		c						
<i>Carex prestlii</i>	i				i						
<i>Carex proposita</i>	i										
<i>Carex rossii</i>	i		w	i	i		w	c			
<i>Carex spectabilis</i>	w	w	w	w	w	c					
<i>Carex stipata</i> var. <i>stipata</i>	i										
<i>Carex subfusca</i>	c	c	c	i	c	i					
<i>Eleocharis macrostachya</i>		w				w					
<i>Scirpus acutus</i> var. <i>occidentalis</i>		c				c					
<i>Scirpus americanus</i>		i				c					
<i>Scirpus maritimus</i>		c				c					
<i>Scirpus microcarpus</i>		i				c					
<i>Scirpus tabernaemontani</i>		c				c					
Juncaceae											
<i>Juncus acuminatus</i>		w				w					
<i>Juncus articulatus</i>		w				w					
<i>Juncus bolanderi</i>		w				w					
<i>Juncus bufonius</i>	i	w				w					
<i>Juncus effusus</i> var. <i>gracilis</i>		c				w					
<i>Juncus ensifolius</i> var. <i>montanus</i>		w				w				w	
<i>Juncus mertensianus</i>	w	w	w	c	i	i	i	i	c	w	i
<i>Juncus nevadensis</i> var. <i>badius</i>			i								
<i>Juncus parryi</i>	w	w	w	w	i	i	c	i	w	w	
<i>Juncus regelii</i>	i	c	i			w				c	
<i>Juncus tenuis</i> var. <i>tenuis</i>	i	w				w					
<i>Luzula hitchcockii</i>	i										
<i>Luzula multiflora</i> ssp. <i>frigida</i>	i										
<i>Luzula parviflora</i>	w	w	w	i	i	i	w	i			
Lemnaceae											
<i>Lemna minor</i>						c					
Liliaceae											
<i>Clintonia uniflora</i>		i	w		i		c	w			
<i>Disporum smithii</i>			c					c			
<i>Lilium columbianum</i>			c								
<i>Maianthemum dilatatum</i>					i			i			
<i>Smilacina racemosa</i>	i		w				i	w			
<i>Smilacina stellata</i>	i	i	c				i	c			
<i>Streptopus amplexifolius</i> var. <i>americanus</i>	i		c								
<i>Trillium ovatum</i> ssp. <i>ovatum</i>			c								
<i>Veratrum viride</i>	i	i	w				i	w			
<i>Xerophyllum tenax</i>	i	i	w				i	i			
Orchidaceae											
<i>Platanthera stricta</i>	i		i								
<i>Spiranthes romanzoffiana</i> var. <i>romanzoffiana</i>	i	i			i	i					
Poaceae											
<i>Achnatherum occidentale</i> ssp. <i>occidentale</i>	c		i	i	i		w	w	i		i
<i>Agrostis capillaris</i> (E)	i				i	i					
<i>Agrostis exarata</i> ssp. <i>exarata</i>	i	w	i		c	w	c	c	c	c	

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
<i>Agrostis exarata</i> var. <i>monolepsis</i>	i	w	i		c	w	c	c	c	c	
<i>Agrostis exarata</i> ssp. <i>minor</i>	i	w	i		c	w	c	c	c	c	
<i>Agrostis gigantea</i> (E)					i	i					
<i>Agrostis pallens</i>	w	w	w	w	c	i	w	w	w	c	
<i>Agrostis scabra</i>	w	i	w	c	w	i	w	i	w	c	i
<i>Agrostis stolonifera</i> (E)					i	i					
<i>Agrostis thurberiana</i>	i	i	i		i	i					
<i>Aira caryophyllea</i> (E)					i						
<i>Alopecurus geniculatus</i>					i	i					
<i>Anthoxanthum odoratum</i> (E)					c	i					
<i>Bromus sitchensis</i> var. <i>sitchensis</i>	i		i		i		i	i			
<i>Calamagrostis canadensis</i> var. <i>canadensis</i>	i	c	i	i		i				c	
<i>Calamagrostis howellii</i>	c										
<i>Calamagrostis sesquiflora</i>	i		i	i							
<i>Cinna latifolia</i>	i	c	i		i	i	i				
<i>Cynosurus echinatus</i> (E)						c					
<i>Dactylis glomerata</i> (E)					c	i					
<i>Danthonia intermedia</i>	i	i			c	i					
<i>Deschampsia atropurpurea</i>	c	i	i	i			i				
<i>Deschampsia danthonioides</i>		i				i					
<i>Deschampsia elongata</i>	c	c			i	c					
<i>Elymus elymoides</i> ssp. <i>elymoides</i>	c		c	c	i		w	i	i	i	i
<i>Elymus glaucus</i> ssp. <i>glaucus</i>	i	i	i		i	i	i	i			
<i>Elymus glaucus</i> ssp. <i>jepsonii</i>	i		i		i	i					
<i>Elymus glaucus</i> ssp. <i>virescens</i>	i	i	c				i				
<i>Elymus trachycaulus</i> ssp. <i>subsecundus</i>	i		i		i						
<i>Festuca arundinacea</i> (E)	i				i	i					
<i>Festuca idahoensis</i> var. <i>idahoensis</i>							i				
<i>Festuca occidentalis</i>	i	i			i	i					
<i>Festuca rubra</i> var. <i>rubra</i>					i	i					
<i>Glyceria elata</i>	i	i			i	i					
<i>Holcus lanatus</i> (E)	i	i			w	w					
<i>Hordeum jubatum</i>		i									
<i>Lolium multiflorum</i> (E)					i						
<i>Lolium perenne</i> (E)					i						
<i>Lolium temulentum</i> (E)					i						
<i>Phleum alpinum</i>	i		i				i	i			
<i>Phleum pratense</i> (E)					i						
<i>Poa compressa</i> (E)		i									
<i>Poa nervosa</i> var. <i>nervosa</i>					i						
<i>Poa pratensis</i> ssp. <i>pratensis</i> (E)					i						
<i>Poa secunda</i> ssp. <i>secunda</i>	w		i	w			i	i			
<i>Poa trivialis</i> (E)					i						
<i>Trisetum canescens</i>	i								i		
<i>Trisetum cernuum</i>	i	i									
<i>Trisetum spicatum</i>	i		i	i	i		i	i	i	i	
<i>Vulpia myuros</i> var. <i>myuros</i> (E)					w	i					
Potamogetonaceae											
<i>Potamogeton foliosus</i> var. <i>macellus</i>			c			c					
<i>Potamogeton natans</i>			c			c					
<i>Potamogeton pectinatus</i>			c			c					
Typhaceae											
<i>Typha latifolia</i>		w				w					

spectabilis Pursh, *Rubus parviflorus* Nutt., *Vaccinium membranaceum* Hook., *Aruncus sylvestris* Kostel., and *Penstemon cardwellii*, and herbs such as *Agrostis pallens*, *Lupinus latifolius*, *Luzula parviflora* (Ehrh.) Desv., *Carex rossii* Boott, and *Anaphalis margaritacea*. Overall, 174 species were

found in the refugia. These areas are quite diverse and contain an assortment of late-successional forest understory species which have persisted since before the eruption as well as barren site species which have invaded the refugia (see del Moral et al. 1995).

Plains of Abraham

The sparse vegetation of the Plains of Abraham is also dominated by those species with seeds that disperse well on the wind. *Anaphalis margaritacea* is the most widespread species, with *Hypochaeris radicata* L., *Epilobium angustifolium*, *Hieracium albiflorum*, *Agrostis pallens* and *Calyptidium umbellatum* (Torrey) E. Greene also common. One *Pinus contorta* Loudon var. *latifolia* Engelm. survived the eruption on the Plains of Abraham. The Plains of Abraham does not contain *Lupinus lepidus* patches and is less diverse than the Pumice Plain with a total of 69 species detected.

Toutle Debris Avalanche

The Toutle Debris Avalanche has numerous and diverse landscapes. Non-native species, from artificial seeding and natural wind-dispersed invasion, dominate much of the mudflow, especially upland environments. Non-native species are less common in wetlands.

Uplands. The uplands are largely dominated by non-native herbaceous species. There are broad areas dominated by *Melilotus alba* Medikus, which was probably a constituent in seed mixes. *Lotus corniculatus* L., *Lotus purshianus* (Benth.) Clements & E. G. Clements var. *purshianus*, *Medicago lupulina* L., *Trifolium pratense* L., and *Trifolium repens* L. are prevalent across the uplands. The annual *Vulpia myuros* (L.) C. Gmelin is also common. *Anaphalis margaritacea*, *Hypochaeris radicata*, *Epilobium angustifolium*, *Epilobium brachycarpum*, *Agrostis pallens*, and *Collomia heterophylla* Hook. are widespread. *Alnus rubra* Bong. stands are prevalent, and *Abies procera* Rehder regeneration is plentiful in places. One hundred and ninety species were found on Toutle Debris Avalanche uplands. The lower elevation, greater proximity to seed sources, and artificial seedings of the Toutle mudflow created conditions which promoted much denser vegetation than is found on the Pumice Plain and Plains of Abraham. In addition, the Toutle River Debris Avalanche is located in a valley below heavily vegetated clearcuts which produce copious quantities of seeds (Dale 1986, 1989).

Wetlands. *Typha latifolia* L. marshes cover many hectares of the mudflow. *Equisetum arvense* carpets broad areas. Dense *Salix sitchensis* thickets are common along streams and around ponds with a wide variety of *Carex* and *Juncus* species. *Spiranthes romanzoffiana* Cham. occurs on wetland edges. One hundred and fifty-six species were found in Toutle Debris Avalanche wetlands.

Toutle Ridge

Toutle Ridge is also occupied by wind-dispersed invasive species similar to those found on the Pumice Plain and Plains of Abraham. Ninety-two species were found on Toutle Ridge uplands. *Sibbaldia*

procumbens L., however, was unique to Toutle Ridge occurring in the high elevation (>1800 m) western portion of the Ridge. Unlike the other species on the Ridge it is a subalpine species (Hitchcock and Cronquist 1973). This species may have invaded from less disturbed ridges to the south or survived the eruption under a thick snow pack in a protected site. The small refugia are dominated by a typical forest understory flora similar to the larger refugia between the Pumice Plain and Plains of Abraham. Ninety-nine species were found in the Toutle Ridge refugia.

Crater

The crater is sparsely vegetated by herbaceous wind-dispersed species similar to those of upland areas of the Pumice Plain and Plains of Abraham. Vegetation, dominated by *Juncus* and *Epilobium* species, is dense in the seepage wetlands. In 1994 the first individual of *Lupinus lepidus* was found in the breach. This was the first large-seeded, non-wind-dispersed species found in the crater since the eruption. The crater proper, which surrounds the lava dome, is very barren. Only a few sparsely distributed, wind-dispersed species have become established. The highly unstable nature of the lava dome limits vegetation over most of the dome. Areas where steam from fumaroles condenses rarely support vascular plants, yet a few individuals of *Hypochaeris radicata* and *Salix sitchensis* were observed. Fifty-two species were found in the breach uplands, 32 species in the breach wetlands, and 17 species in the high crater.

Non-native Species

The second most widespread invader of upland successional landscapes on the Pumice Plain, Plains of Abraham, and Toutle Ridge (the most widespread is *Anaphalis margaritacea*) is the non-native *Hypochaeris radicata*. It is possible that the rate of succession has changed substantially because of the presence of this non-native species. Most of the other exotics, such as *Cirsium*, *Senecio*, and *Sonchus* species, do not dominate the landscape. Non-natives are less common in wetlands. The only *Cytisus scoparius* (L.) Link plant was located on the west edge of the Pumice Plain and was chopped down in 1994. *Cytisus scoparius* forms dense thickets on the Toutle Debris Avalanche outside of the range of this study. In all, 57 non-native species were found.

The Toutle River Debris Avalanche has vast areas completely dominated by non-native species to the complete exclusion of natives presumably due to the artificial seeding that was undertaken after the eruption for erosion control. Species such as *Lotus corniculatus*, *Medicago lupulina*, *Melilotus alba*, *Trifolium pratense*, *Trifolium repens*, and *Vulpia myuros* cover large areas of the Debris Avalanche. These species create extensive monocul-

tures which exclude native species and prevent natural successional processes from occurring. For example, the entire mouth of Coldwater Lake is completely dominated by non-native species. Thus, the possibility of natural succession to a scrub-shrub or forested wetland lakeshore is reduced. Other non-natives on the lahar, such as *Hypericum perforatum* L., *Rubus discolor* Weihe & Nees, *Cirsium arvense* (L.) Scop., and *Cirsium vulgare* (Savi) Ten., probably arrived on their own via wind or animal dispersal.

CONCLUSION

The focus of this study was to investigate the recently devastated areas of Mount St. Helens. Species richness is difficult to compare with studies of other Cascade Range volcanoes in which the entire volcano, including relatively undisturbed areas, was surveyed. These other Cascade Range volcanoes have not been subjected to recent volcanic eruptions.

Because areas investigated during the study varied greatly in terms of current physical features, environmental conditions and size of area available for colonization, species richness varied across the landscape. The highest richness was observed in the Toutle Debris Avalanche uplands, probably due to the area's great size, diversity of physical features and proximity to seed sources of potential colonizers.

Richness on Mount St. Helens has increased greatly since 1980 when richness equaled zero (except in the refugia). Although most of the species currently dominant on the landscape are invasive species that characteristically have small wind-dispersed seeds, some large seeded plants such as *Lupinus lepidus* are common. No threatened, endangered or sensitive species or regional endemics were detected during our survey of the volcano. An interesting finding was the presence of *Salix exigua*. This species is not thought to occur west of the Cascades. The open primary successional habitats created by the volcanic eruption allow colonization by wind-dispersed species from great distances.

This study creates a baseline to judge changes to the landscapes of Mount St. Helens, and should also facilitate future studies of primary successional processes on the mountain.

ACKNOWLEDGMENTS

Thanks to all the following people who contributed to this project. Roger del Moral and Dave Wood provided useful comments on the species list and manuscript. Paul Yurky contributed time and effort to all aspects of this project. Michele Glazer improved the manuscript. Sarah Gage of University of Washington herbarium and Scott Sundberg of Oregon State University herbarium checked the species list for taxonomic correctness. Shiro Tsuyuzaki, Mandy Tu, John Bishop and Peter Chilson provided companionship in the field and assisted in plant collections. JoEllen VanDeMark and Betsy Lyons assisted with

plant identification. Difficult taxa were verified by Alan Yen (Cyperaceae), John Christy (aquatics), Ed Alverson (ferns), George Argus (Salicaceae), Thomas Hinckley (Pinaceae), Joe Arnett (*Silene*), and Sarah Gage (problem id's). Brian Haber created the figure used in this publication. Also, thanks to two anonymous reviewers. A grant from the Washington Native Plant Society made this project possible. NSF Grants BSR-89-06544 and DEB-9406987 to Roger del Moral were also of assistance.

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